

Anatomical and behavioural studies on vision in *Nautilus* and *Octopus*

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Abstract. *Nautilus* is a cephalopod that is primitive in many respects, and is often considered to be a "living fossil". The eye of *Nautilus* is apparently a primitive feature, acting as a pin-hole camera and lacking any lens or other dioptric apparatus. In contrast, in *Octopus* and most other coleoid cephalopods, there is a well formed spherical lens. The basic structure of the retina is similar in the two animals, but there are also a number of important differences: the microvilli of the receptors of *Nautilus* do not form a regular rectilinear array as they do in *Octopus*; the microvilli from neighbouring receptors overlap, which does not occur in *Octopus*; the supporting cells have a different structure; the nuclei of the supporting cells and receptor cells are distributed either side of the basement membrane in *Octopus*, but not in *Nautilus*; cilia are present in the retina of *Nautilus* but not *Octopus*; and the myeloid bodies are much more developed in *Nautilus*.

Both behavioural experiments and calculation show that, as expected on anatomical grounds, visual acuity and sensitivity are much better in *Octopus* than *Nautilus*. Reasons for the limitations in the visual capabilities of the two animals are discussed.

Nautilus is the last surviving genus of a group that arose in the Triassic, and has apparently changed little since Cretaceous times, at least as far as we can judge from the shell. The animal shows many apparently primitive features, such as the lack of an ink sac or chromatophores, the external shell, the funnel formed of two overlapping lobes, and the simple pin-hole camera eye lacking any lens or other dioptric apparatus (e.g. Morton, 1967). The ancestry of the genus has been discussed by, among others, Teichert and Matsumoto (1987), who concluded that it can truly be called a "living fossil".

The first octopods, on the other hand, are found in the Upper Cretaceous (Donovan, 1977), and the group must be counted among the most developed invertebrates in existence. The octopus eye, which resembles that of most other coleoid cephalopods, has in contrast to *Nautilus* a very well-developed lens and superficially looks remarkably similar to the eyes of vertebrates. The present paper compares the structure and function of the eyes of these two very different cephalopods.

STRUCTURE OF THE EYE IN *NAUTILUS* AND *OCTOPUS*

The most obvious difference between the eyes of *Nautilus* and *Octopus* is the complete lack of any dioptric apparatus in the former genus. The pupil in *Nautilus* opens directly to the sea, and the eye must act as a pin-hole camera. The eyes of octopuses in contrast have well developed spherical lenses, which, as in most fishes, have focal lengths

about 2.5 times their radius (Matthiessen's ratio) and are well corrected for spherical aberration (Sivak, 1982; Sroczyński and Muntz, 1985). The overall size of the eyes of the two animals is, however, similar, and both animals have contractile pupils that are elongated in the horizontal direction (Muntz, 1977; Hurley *et al.*, 1978). Figure 1 shows the general appearance of the eyes of *Nautilus pompilius* Linnaeus and *Octopus vulgaris* Lamarck.

Descriptions of the retinal anatomy of *Nautilus* can be found in Barber and Wright (1969), Muntz and Raj (1984), and Muntz and Wentworth (1987); and of *Octopus* in Young (1962a, 1971) and Yamamoto *et al.* (1965). These papers also give references to earlier work. Following convention, in this paper the segments of the receptors facing the light, which contain the photopigment, will be referred to as the distal or outer segments, and the nuclear region as the proximal or inner segment.

The basic elements of the retina in both *Octopus* and *Nautilus* are the receptor cells, with distal segments consisting of a central core from which the microvilli (which contain the visual pigment) radiate outwards, and the supporting cells with their processes lying between the receptor cell outer segments (Figs. 2, 3). The packing of the receptor cells is roughly similar in the two species. Thus, there are about 20,000 receptor cells mm⁻² in *N. pompilius*, varying little over the retina (Muntz and Raj, 1984), and between 18,000 and 55,000 mm⁻² in *O. vulgaris*, depending on retinal position (Young, 1971). Although basically similar, there are however also a number of important differences between the two species, which can be summarised as follows.

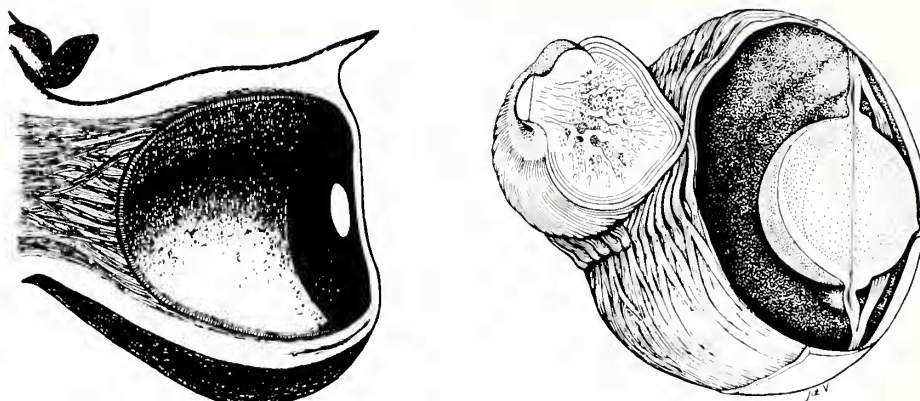


Fig. 1. Left, vertical section through the eye of *Nautilus* (from Willey, 1902). Right, vertical section through the eye and optic lobe of *Octopus* (from Young, 1962b).

(i) Transverse sections through the outer segments of the retinal receptors of *Nautilus* show that there are usually five or six (occasionally four or seven) bundles of microvilli running out from each receptor body to the bodies of neighbouring receptors. The receptors thus form a roughly hexagonal array (Fig. 2a). The microvilli from neighbouring receptors within a given bundle often interdigitate, although the extent of this interdigitation is not clear. The processes of the supporting cells run out in groups between these bundles of microvilli.

In contrast in *Octopus* the receptor outer segments form a rectilinear array, with the microvilli oriented vertically or horizontally with respect to gravity (Fig. 3a). The microvilli of each receptor remain strictly segregated from those of the neighbouring receptors, with no interdigitation.

(ii) The structure of the supporting cells is quite different in the two animals. In *Nautilus* each cell has a number of fine microvillous processes which project out between the receptor outer segments in groups, whereas in *Octopus* each supporting cell has a single process, which is much larger and contains screening pigment. In the former animal the cell nuclei of both the receptors and the supporting cells lie distal to the basement membrane, whereas in *Octopus* the supporting cell nuclei lie distal and the receptor cell nuclei proximal to the basement membrane.

(iii) In *Nautilus* the supporting cells have cilia, as well as the microvillous processes that extend between the receptors. It is not certain whether the receptor cells have cilia as well. Ciliary structures have not been reported in the retina of any other adult cephalopod, although the photosensitive organs of many animals have receptors of ciliary origin, or cilia, presumed not to be photosensitive, intermingled with the receptors (Vanfleteren, 1982).

(iv) The inner segments of *Nautilus* photoreceptors have complex myeloid bodies, which often have the appearance of a tubular structure, or a series of wavy plates (Fig. 2). It has been argued that this apparently complex structure consists of a series of dimpled plates, stacked in register

above each other (Muntz and Wentworth, 1987). In *Octopus* and the other coleoid cephalopods, the myeloid bodies are reduced to a few membranous strands.

It is interesting that some of the characteristics by which the *Nautilus* retina differs from that of adult octopuses also have been found during the development of the embryos of coleoid cephalopods. Thus in the cuttlefish *Sepiella japonica* Sasaki, embryos have cilia on both receptor and supporting cells, the nuclei of both the receptor cells and the supporting cells lie distal to the basement membrane, and the supporting cells send long microvillous processes out among the whole length of the receptor outer segments (Yamamoto, 1985). Work in progress shows a similar situation in the embryos of the Australian octopuses *Octopus pallidus* Hoyle and *O. australis* Hoyle (Wentworth and Muntz, unpub. data).

BEHAVIOURAL STUDIES

To date, no studies of vision have been carried out with *Nautilus* using any form of learnt behaviour, and it is not known how far the animals are capable of learning. However, *Nautilus* shows two well developed forms of innate visual behaviour, the positive phototactic response and the optomotor response, which have been used to determine the animals' visual acuity, and also their absolute and spectral sensitivities (Muntz and Raj, 1984; Muntz, 1986, 1987).

As we should expect for an animal with an eye having the simple optics of a pin-hole camera, visual performance in *Nautilus* is very poor compared to that of animals with lens bearing camera eyes. The minimum separable visual acuity, for example, measured using the optomotor response, lies between 5.5° and 11.25°, which agrees well with values calculated on the basis of the gross dimensions of the eye and pupil, and with expectations based on photographing a visual test chart using a scale model of the eye (Muntz and Raj, 1984). This can be compared with values of about 5°

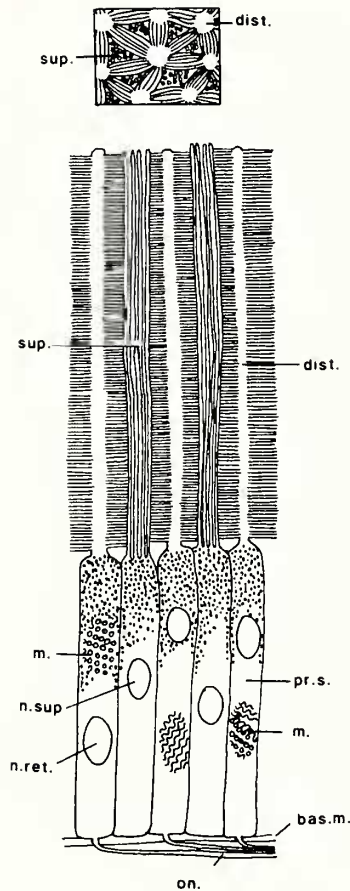


Fig. 2. Diagram of the structure of the retina of *Nautilus*, as seen in tangential (above) and radial section (below). The diagram is not to scale: in particular the horizontal dimensions have been exaggerated compared to the vertical dimensions for clarity. The mean length of the distal segments is in fact about $360\ \mu\text{m}$, and of the proximal segments $100\ \mu\text{m}$, and the mean centre to centre distance between adjacent receptors $3.5\ \mu\text{m}$: there is little variation over the retina (bas.m., basement membrane; dist., receptor distal segment with microvilli radiating from a central core; pr.s., receptor proximal segment; sup., processes of supporting cells; m., myeloid body; on., optic nerves; n.sup., nucleus of supporting cells; n.ret., nucleus of retinal cell).

obtained with octopuses, various fishes and two aquatic mammals (Table 1): even with the most favourable estimate of 5.5^0 the performance level of *Nautilus* is over 60 times worse than for these other aquatic animals.

By using the positive phototactic behaviour of *Nautilus* it has also been possible to determine its absolute sensitivity to tungsten light (Muntz, 1987). In itself this result is not particularly useful, because the spectral output of the tungsten source used was very different from that of the light to which the animal will be exposed in its natural environment. However, given a knowledge of the spectral transmission of the water in which the animals live, the spectral quality of the daylight reaching the surface of the sea, and the animals' own spectral sensitivity, it is possible from these results to

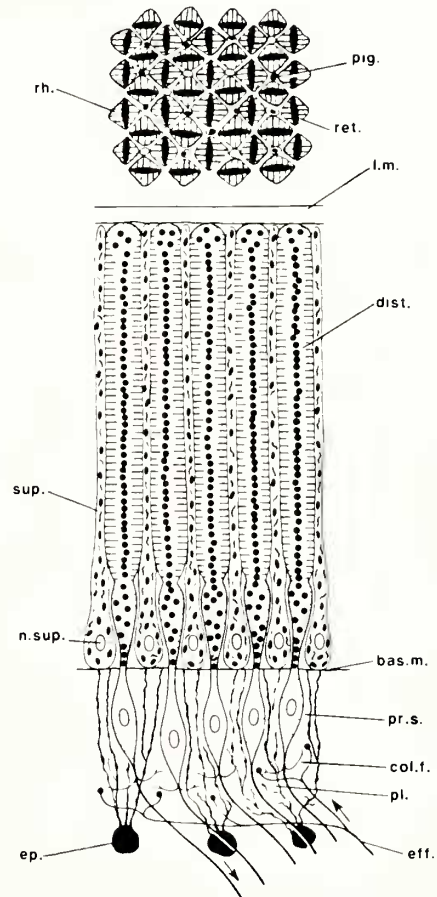


Fig. 3. Diagram of the structure of the retina of *Octopus*, as seen in tangential (above) and radial section (below), from Young (1962a). Not to scale: in fact the distal segments vary between about $60\ \mu\text{m}$ and $180\ \mu\text{m}$ in length depending on retinal position, while the proximal segments are about $90\ \mu\text{m}$ long and the individual rhabdomeres about $5\ \mu\text{m}$ in width (Young, 1962a) (rh., rhabdome; pig., pigment granule at centre of rhabdome; ret., retinal cell; l.m., limiting membrane; dist., distal segment of receptor; bas.m., basal membrane; pr.s., proximal segments of retinal cells; col.f., fine dendritic collateral of retina cell; pl., retinal nerve plexus; eff., ending of efferent fibre in retina; ep., epithelial cell; n.sup., nuclei of supporting cells; sup., processes of supporting cells).

calculate the maximum depth at which surface light would be visible at all to *Nautilus*. Reasonable estimates for the first two factors are available, and the animals' spectral sensitivity was taken to be the same as the absorption spectrum of its visual pigment (see Muntz, 1987 for details). It appears that some daylight should be visible to *Nautilus* down to 800 m, which is slightly deeper than the maximum depth at which the animal is found. This is, however, considerably less than the maximum depth at which daylight should be visible to deep sea fishes, which has been calculated by Clarke and Denton (1962) as over 1000 m. Calculations based on the dimensions of the *Nautilus* eye also indicate that *Nautilus* will be less sensitive, by about 2 log units, than a fish or cephalopod that has a camera eye with a lens obeying

Matthiessen's ratio (Muntz and Raj, 1984).

Finally, the positive phototactic behaviour has also been used to determine spectral sensitivity directly (Muntz, 1986). The sensitivity curve obtained agreed well with the absorption spectrum of the extractable visual pigment, which was itself well fitted by Dartnall's (1953) visual pigment nomogram for an A_1 -based pigment with its maximum at 467 nm.

In contrast to *Nautilus*, octopuses learn visual discriminations very readily, and a great deal of information is now available on their visual capabilities (Wells, 1978; Messenger, 1981 for reviews). Most of this work has concerned higher visual functions, such as the ability to discriminate shapes, the mechanisms by which such discriminations are learnt, and the function of the various parts of the central nervous system. Comparatively little work has been done on the animals' more basic visual capabilities, such as sensitivity or visual acuity, which are probably more directly related to the optics of the eye and the structure and function of the retina, and which can be compared to the data that are available for *Nautilus*. In the case of sensitivity, for example, there appear to have been no studies at all carried out on coleoid cephalopods using learning, and only one study involving innate behaviour, in which the spectral sensitivity of *Loligo pealei* Lesueur larvae was measured using the positive phototactic response in a manner rather similar to that used with *Nautilus*. The results were also similar show-

ing a smooth bell-shaped spectral sensitivity curve maximal at around 480 nm and compatible with a single visual pigment (White, 1924).

A few behavioural studies have been carried out on the visual acuity of octopuses. Thus Sutherland (1963), using a training situation, obtained an estimate of 17' for *Octopus vulgaris*, and Packard (1969), using the same species and the optomotor response, found that in very small specimens (<3-22g) acuity improved with size. The most recent studies on acuity in octopuses (Muntz and Gwyther, 1988a, 1989) used fully grown animals and a two choice learning situation, and the stimuli were gratings of equally spaced black and white stripes oriented vertically, horizontally, or obliquely at 45°. The animals were trained to discriminate these gratings from each other or from a uniform gray stimulus, and visual acuity was taken as the separation between the bars of the gratings where performance reached chance levels. The results showed that the minimum separable visual acuity of *O. australis* and *O. pallidus* is about 5' (Fig. 4). With gratings close to the animals' threshold, performance with the vertical gratings was best, and with the horizontal gratings worst, but the effect was not large.

The ability of *Octopus pallidus* and *O. australis* to discriminate distances has also been determined behaviourally, using the animals' tendency to attack the nearer of two stimuli presented simultaneously (Muntz and Gwyther, 1988b). Assuming that the animals are using accommoda-

Table 1. Minimum separable visual acuities, in minutes of arc, of various aquatic animals measured behaviourally using gratings. Learnt discriminations were used in all cases except *Nautilus* where the optomotor response was used.

Species	Acuity	Reference
MAMMALS		
Harbour seal <i>Phoca vitulina</i> Linnaeus	8.3	Schusterman and Balliet, 1970
Stellar Sea Lion <i>Eumetopias jubata</i> (Schreber)	7.1	Schusterman and Balliet, 1970
TELEOST FISHES		
Convict fish <i>Microcanthus strigatus</i> (Cuvier and Valenciennes)	4.9	Yamanouchi, 1956
Minnow <i>Phoxinus laevis</i> Linnaeus	10.8	Brunner, 1934
Skipjack tuna <i>Katsuwomis pelamis</i> Linnaeus	5.5	Nakamura, 1968
Little tuna <i>Euthynnus affinis</i> (Cantor)	7.4	Nakamura, 1968
Cichlid fish <i>Aequidens portalegrensis</i> (Hensel)	5.8	Baerends <i>et al.</i> , 1960
CEPHALOPODS		
<i>Nautilus</i> <i>Nautilus pompilius</i>	330-670	Muntz and Raj, 1984
Octopus <i>Octopus pallidus</i> <i>O. australis</i>	5.0	Muntz and Gwyther, 1988a

tion to estimate distance, which various tests indicated is the most likely mechanism, the animals can detect blurring of points on the retinal image comparable in size to a single retinal receptor, and lens displacements of around 10 μm .

Finally, training experiments have shown that *Octopus vulgaris* can discriminate the plane of polarised light (Moody and Parriss, 1961), and also it has been shown that two species of decapod larvae orient themselves to the plane of polarised light (Jander *et al.*, 1968). It is not known whether *Nautilus* has this ability.

DISCUSSION

The evolution of the camera eye has attracted interest ever since Darwin [1859 (reprinted 1958)] listed it as one of the "organs of extreme perfection and complication", and wrote that to believe that such organs could have been formed by natural selection seems "absurd in the highest possible degree". Darwin's solution to the problem was to suggest that the eye must have arisen through numerous inheritable gradations, each of which was useful to its possessor, and that while strictly we should look for such gradations among the animal's lineal ancestors, we are usually forced to look at living species of the same group to see what gradations are possible.

The eye of *Nautilus* could be taken as such a gradation on the route to the complex eyes of the more recent

cephalopods. Even though *Nautilus* vision is poor, nevertheless its visual behavior is precise, in that in the optomotor response they follow the stripes accurately without visible lag, and in the phototactic situation if the difference between the stimuli is well above threshold the brighter light is chosen on every occasion. The eyes are also stabilised with respect to gravity by means of the statocysts (Hartline *et al.*, 1979). These facts suggest that vision is important to the animal. It is not, however, clear what use they make of such poor vision in their normal life. The habitat of *Nautilus* often has strong currents, and the optomotor behaviour could be related to holding station under these conditions. It could also be that the positive phototactic behaviour is related to bioluminescence, which is a major source of light at depth in the sea. *Nautilus* is often trapped in association with deep water bioluminescent shrimps, which also feed on decaying animal material, and moving towards bioluminescence could help take the animals towards their food. Finally, *Nautilus* shows diurnal vertical migrations (Carlson *et al.*, 1984; Ward *et al.*, 1984), and vision could be a factor in this behaviour. Without further information on the normal behaviour of the animals however, these remain speculations.

In the case of *Octopus* we have no behavioural evidence on its visual sensitivity, although presumably it is considerably better than that of *Nautilus*. The minimum separable visual acuity of 5' for *Octopus* is comparable to that of fishes and aquatic mammals (Table 1). Nevertheless, it is not clear why the acuity is not even better than this. The retinal mosaic is rather finer than necessary for the acuity that is in fact achieved (Muntz and Gwyther, 1988a), and the pupil size is large enough that diffraction will not be limiting. In *Eledone cirrhosa* (Lamarck), another octopod, spherical aberration is far less than would be needed to limit acuity to this level (Sroczyński and Muntz, 1985). Furthermore, terrestrial animals can achieve much better acuities; in the case of humans, for example, the minimum separable lies between 0.5' and 1' (e.g. Senders, 1948), and in the American kestrel, *Falco sparverius* Linne', the acuity, measured behaviourally using square wave gratings, is 0.19' (Fox *et al.*, 1976). Since, however, the minimum separable acuity, measured behaviourally, has been found to be about 5' for all aquatic animals where it has been measured, it could be the environment itself that is limiting. While not very many data are available on the subject, it is clear that high spatial frequencies are particularly heavily attenuated by the water body itself, and it could be that the ability to resolve very fine detail is consequently irrelevant (see Muntz, 1990 for further discussion).

The ability of octopuses and other coleoid cephalopods to discriminate the plane of polarisation of light is usually attributed to the regular rectilinear array of the microvilli of their receptors (Moody and Parriss, 1961). *Nautilus* lacks such a rectilinear array. Nevertheless, the microvilli within any

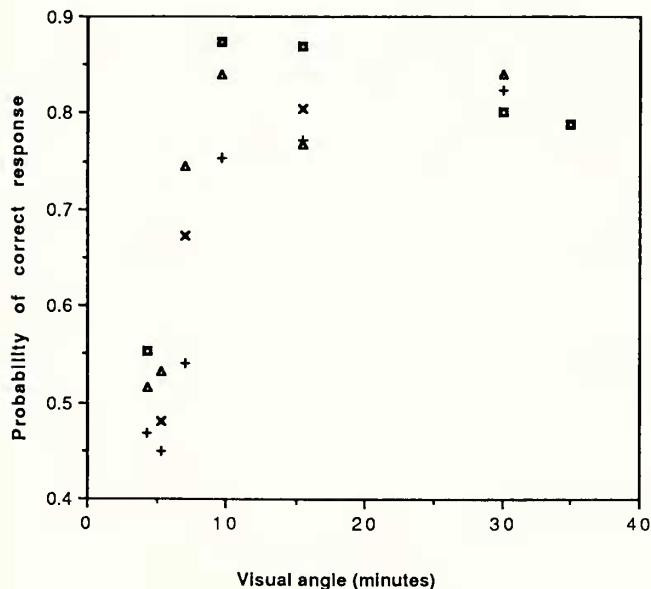


Fig. 4. Visual acuity of *Octopus*, measured behaviourally for various stimulus combinations. The animals weighed between 59 and 1134g. ▲, vertical gratings against grey; +, horizontal gratings against grey; X, oblique gratings against grey; ■, vertical gratings against horizontal gratings. Data from Muntz and Gwyther (1988a, 1989).

given bundle remain parallel to each other, and so plane polarised light should still be able to affect the receptors differentially, even though there would be no precise relationship between the plane of polarisation and the receptors stimulated. It would be interesting to know whether *Nautilus* can show any differential response to polarised light.

LITERATURE CITED

- Baerends, G. P., B. E. Bennema and A. A. Vogelzang. 1960. Über die Änderung der Sehschärfe mit dem Wachstum bei *Aequidens portalegrensis* (Hensel) (Pisces, Cichlidae). *Zoologische Jahrbücher* 88:67-78.
- Barber, V. C. and D. E. Wright. 1967. The fine structure of the sense organs of the cephalopod mollusc *Nautilus*. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 102:293-312.
- Brunner, G. 1934. Über die Sehschärfe der Elritze (*Phoxinus laevis*) bei verschiedenen Helligkeiten. *Zeitschrift für vergleichende Physiologie* 21:296-316.
- Carlson, B. A., J. N. McKibben and M. V. DeGruy. 1984. Telemetric investigation of vertical migration of *Nautilus belauensis* in Palau (Western Caroline Islands, Pacific Ocean). *Pacific Science* 38:183-188.
- Clarke, G. L. and E. J. Denton. 1962. Light and animal life. In: *The Sea*, Vol. 1, M. N. Hill, ed. pp. 456-468. John Wiley, New York.
- Dartnall, H. J. A. 1953. The interpretation of spectral sensitivity curves. *British Medical Bulletin* 9:24-30.
- Darwin, C. 1958. *The Origin of Species*. Reprint of 1st edition (1859), J. W. Burrow, ed. Penguin Books, Harmondsworth. 477 pp.
- Donovan, D. T. 1977. In: *Symposium on the biology of cephalopods*, M. Nixon and J. B. Messenger, eds. *Symposia of the Zoological Society of London* 38:277-285.
- Fox, R., S. W. Lehmkuhle and D. H. Westendorf. 1976. Falcon visual acuity. *Science* 192:263-265.
- Hartline, P. H., A. C. Hurley and G. D. Lange. 1979. Eye stabilization by statocyst mediated oculomotor reflex in *Nautilus*. *Journal of Comparative Physiology* 132:117-1226.
- Hurley, A. C., G. D. Lange and P. H. Hartline. 1978. The adjustable "pinhole camera" eye of *Nautilus*. *Journal of Experimental Zoology* 205:37-44.
- Jander, R., K. Daumer and T. H. Waterman. 1963. Polarised light orientation by two Hawaiian decapod cephalopods. *Zeitschrift für vergleichende Physiologie* 46:383-394.
- Messenger, J. B. 1981. Comparative physiology of vision in molluscs. In: *Handbook of Sensory Physiology*, vol. VII/6C, *Comparative physiology and evolution of vision in invertebrates*, H. Autrum, ed. pp. 93-200. Springer-Verlag: Berlin, Heidelberg, New York.
- Moody, M. F. and J. R. Parriss. 1961. The discrimination of polarised light by *Octopus*: A behavioural and morphological study. *Zeitschrift für vergleichende Physiologie* 44:269-291.
- Morton, J. E. 1967. *Molluscs* (4th edition). London. Hutchinson. 244 pp.
- Muntz, W. R. A. 1977. Pupillary responses of cephalopods. In: *Symposium on the biology of cephalopods*, M. Nixon and J. B. Messenger, eds. *Symposia of the Zoological Society of London* 38:277-285.
- Muntz, W. R. A. 1986. The spectral sensitivity of *Nautilus pompilius*. *Journal of Experimental Biology* 126:513-517.
- Muntz, W. R. A. 1987. Visual behaviour and visual sensitivity of *Nautilus pompilius*. In: *The biology and paleobiology of a living fossil*. W. B. Saunders and N. H. Landman, eds. pp. 231-244. Plenum Press, New York.
- Muntz, W. R. A. (1990). Stimulus, environment and vision in fishes. In: *The visual system of fish*. R. H. Douglas and M. B. A. Djamgoz, eds. pp. 491-511. Chapman and Hall, London.
- Muntz, W. R. A. and J. Gwyther. 1988a. Visual acuity in *Octopus pallidus* and *Octopus australis*. *Journal of Experimental Biology* 134:119-129.
- Muntz, W. R. A. and J. Gwyther. 1988b. Visual discrimination of distance by octopuses. *Journal of Experimental Biology* 140:345-355.
- Muntz, W. R. A. and J. Gwyther. 1989. The visual acuity of octopuses for gratings of different orientations. *Journal of Experimental Biology* 142:461-464.
- Muntz, W. R. A. and U. Raj. 1984. On the visual system of *Nautilus pompilius*. *Journal of Experimental Biology* 109:253-263.
- Muntz, W. R. A. and S. L. Wentworth. 1987. An anatomical study of the retina of *Nautilus pompilius*. *Biological Bulletin* 173:387-397.
- Nakamura, E. L. (1968). Visual acuity of two tunas, *Katsuwonus pelamis* and *Euthynnus affinis*. *Copeia* 1:41-49.
- Packard, A. (1969). Visual acuity and eye growth in *Octopus vulgaris* (Lamarck). *Monitore Zoologica Italiana (N.S.)* 3:19-32.
- Schusterman, R. J. and R. F. Balliet. 1970. Visual acuity of the harbour seal and the stellar sea lion underwater. *Nature, London* 226:563-564.
- Senders, V. L. (1948). The physiological basis of visual acuity. *Psychological Bulletin* 45:465-490.
- Sivak, J. G. 1982. Optical properties of a cephalopod eye. *Journal of Comparative Physiology* 147A:323-327.
- Sroczyński, S. and W. R. A. Muntz. (1985). Image structure in *Eledone cirrhosa*, an octopus. *Zoologische Jahrbücher* 89:157-168.
- Sutherland, N. S. (1963). Visual acuity and discrimination of stripe widths in *Octopus vulgaris* Lamarck. *Pubblicazioni Stazione Zoologica Napoli* 33:92-109.
- Teichert, C. and T. Matsumoto. 1987. The ancestry of the genus *Nautilus*. In: *Nautilus: The Biology and Paleobiology of a Living Fossil*. W. B. Saunders and N. H. Landman, eds. pp. 25-32. Plenum Press, New York.
- Vanfleteren, J. R. 1982. Monophyletic line in evolution? Ciliary induced receptor membranes. In: *Visual Cells in Evolution*. J. A. Westfall, ed. pp. 107-136. Raven Press, New York.
- Ward, P. D., B. Carlson, M. Weekley and B. Brumbaugh. 1984. Remote telemetry of daily vertical and horizontal movement by *Nautilus* in Palau. *Nature, London* 309:248-250.
- Wells, M. J. 1978. *Octopus: Physiology and Behaviour of an Advanced Invertebrate*. London: Chapman and Hall. 417 pp.
- White, G. M. 1924. Reactions of the larve of the shrimp, *Palaemonetes vulgaris*, and the squid, *Loligo pealii*, to monochromatic light. *Biological Bulletin* 47:265-273.
- Wille, A. 1902. *Contribution to the natural history of the pearly Nautilus: Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897*: Part 6:691-683. University Press Cambridge, England.
- Yamamoto, T. 1985. Ontogeny of the visual system in the cuttlefish, *Sepiella japonica*. I. Morphological differentiation of the visual cell. *Journal of comparative Neurology* 232:347-361.
- Yamamoto, T., K. Tadaki, Y. Sugarara and A. Tonosaki. 1965. Fine structure of the octopus retina. *Journal of Cell Biology* 25:345-365.
- Yamanouchi, T. 1956. The visual acuity of the coral fish *Microanthus strigatus* (Cuvier and Valenciennes). *Publications of the Seto Marine Biology Laboratories* 5:133-156.
- Young, J. Z. 1962a. The retina of cephalopods and its degeneration after optic nerve section. *Philosophical Transactions of the Royal Society of London* B245:1-18.
- Young, J. Z. 1962b. The optic lobes of *Octopus vulgaris*. *Philosophical Transactions of the Royal Society of London* B245:19-58.
- Young, J. Z. 1971. *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford University Press. 690 pp.